THE SKULL OF THE CALLOVIAN PLESIOSAUR *CRYPTOCLIDUS EURYMERUS*, AND THE SAUROPTERYGIAN CHEEK

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ABSTRACT. Mechanical preparation of a relatively complete new skull specimen of *Cryptoclidus eurymerus* has revealed the palate and cheek regions for the first time, permitting a more accurate reconstruction to be given. The wider phylogenetic implications of differing cheek and orbit configurations in sauropterygians are discussed and a cladogram given: the Cryptoclididae and the remaining plesiosauroids are sister groups; deep ventral cheek excavation arose through loss of the diapsid lower temporal arch and is a shared derived character of cryptoclidids, whereas an enlarged orbit and narrow vertical jugal bar are apomorphies. The palatal and mandibular structure of *Cryptoclidus* is derived in comparison with pliosauroids: coronoids, prearticulars, suborbital fenestrae and the large pterygoid flange are all absent. These differences relate to feeding habit: *Cryptoclidus* fed on small soft-bodied prey, and shows no adaptations for resisting torsional forces upon the jaws. Underwater olfaction similar to the pliosauroid system may have been present in *Cryptoclidus*.

THE structure of the skull in plesiosauroid specimens from soft clays is often deficient in delicate areas due to poor preservation, rough collection and subsequent handling. In particular, the cheek and skull roof of the Callovian genus *Cryptoclidus* from the English Lower Oxford Clay have of necessity been reconstructed from deficient specimens (Andrews 1910; Brown 1981*b*).

On 4th September 1987 a new and almost complete specimen of *Cryptoclidus eurymerus* was discovered at Dogsthorpe, near Peterborough, UK (Martill 1988). The skull was collected in a moist clay block supported by a plaster jacket, and was then removed to the laboratory of Leicestershire Museum and Art Gallery. The plaster jacket was replaced by a double-sided silicone rubber support, and the specimen was prepared (by A.R.I.C.) using mechanical methods including an 'Airbrasive' machine. Breaks were repaired with acetone-soluble plastics. Although nevertheless distorted and incomplete due to post mortem crushing and drop-out, the specimen is the best known skull of *Cryptoclidus*.

SYSTEMATIC PALAEONTOLOGY

Abbreviations used. BMNH, Palaeontology Collections, Natural History Museum, Cromwell Road, London SW7 5BD. Previously the British Museum (Natural History). PETMG, Geological Collections, Peterborough City Museum and Art Gallery, Priestgate, Peterborough PE1 1LF.

Subclass SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Superfamily PLESIOSAUROIDEA (Gray, 1825) Welles, 1943
Family CRYPTOCLIDIDAE Williston, 1925

Diagnosis. See Brown (1994).

Genus CRYPTOCLIDUS Seeley, 1892

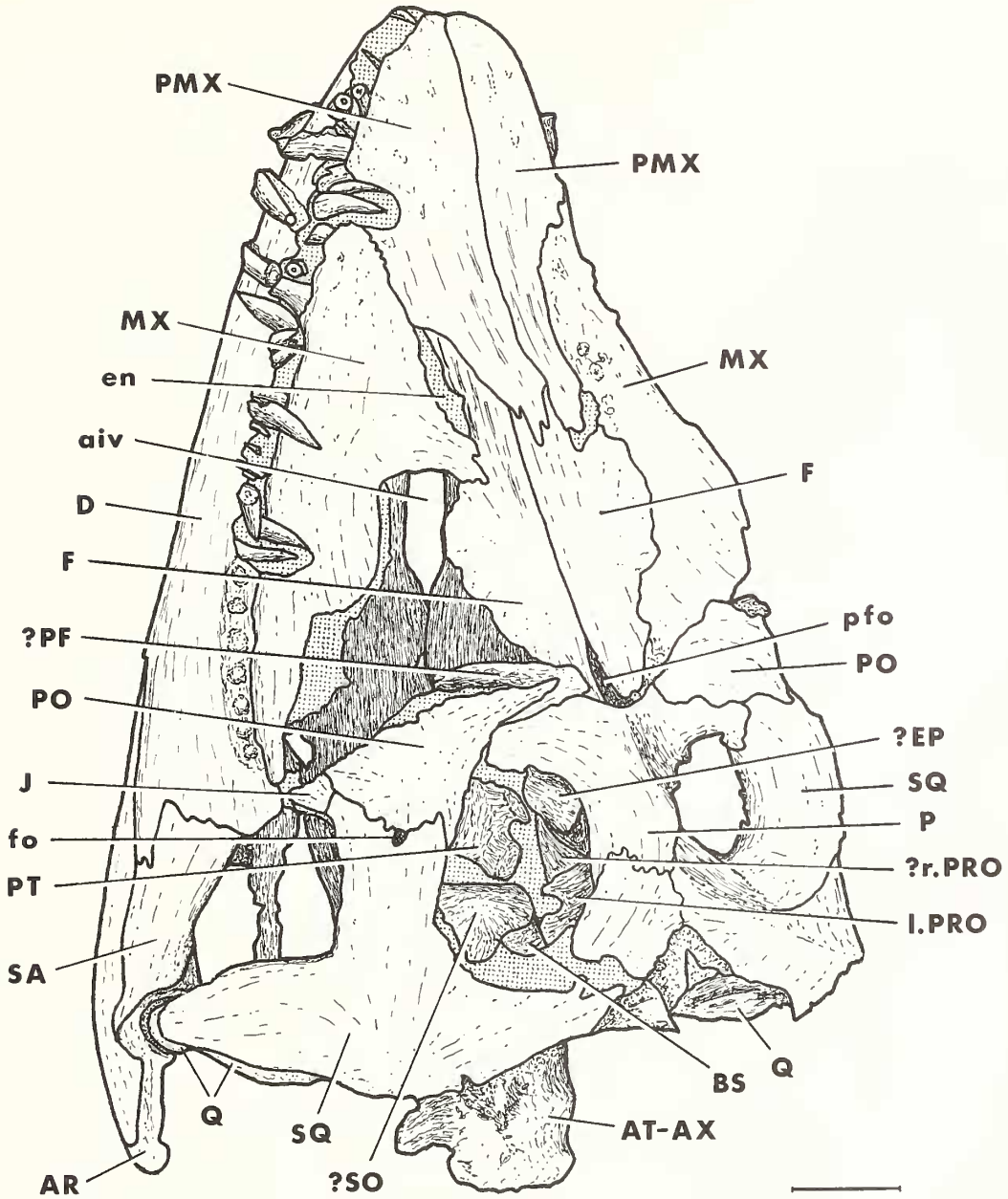*Type species. Cryptoclidus eurymerus* (Phillips, 1871) from the Lower Oxford Clay of Peterborough, UK.
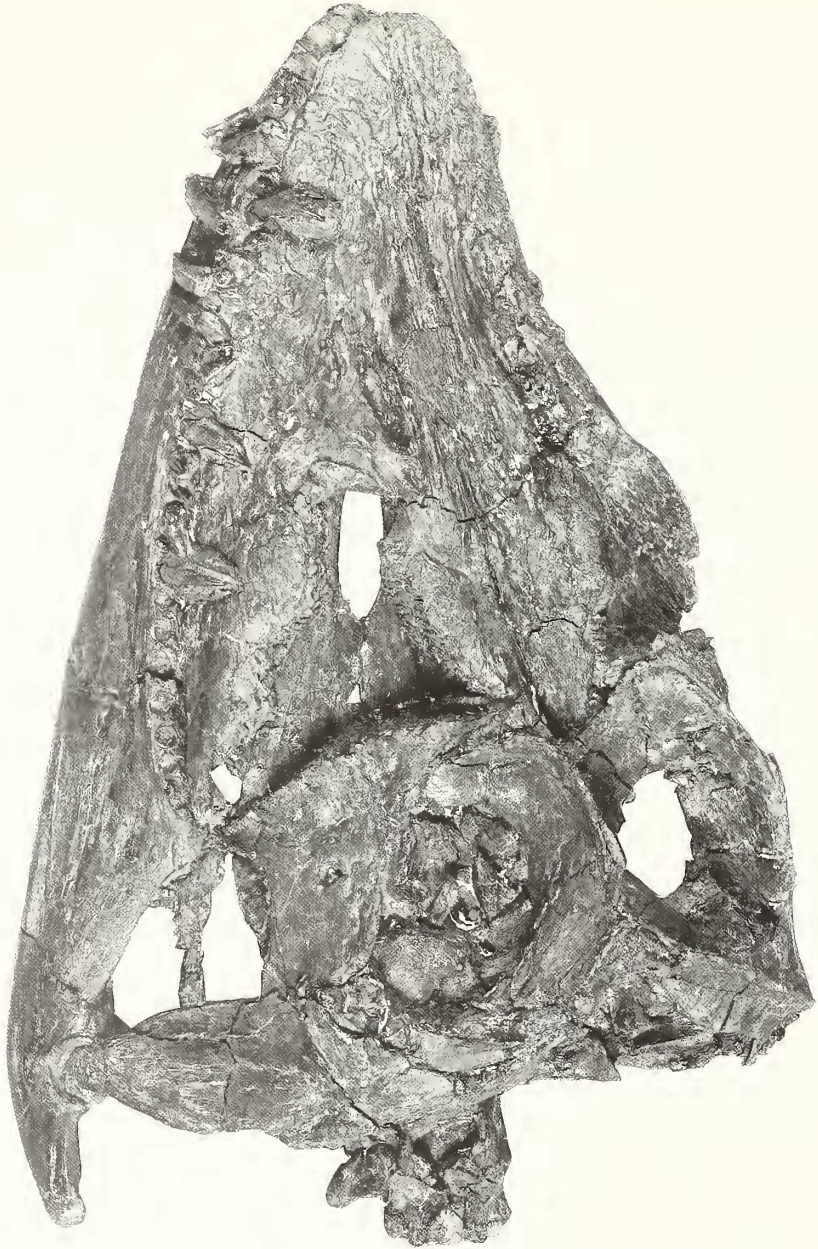
TEXT-FIG. 1. *Cryptoclidus eurymerus* (Phillips). PETMG R.283.412; dorsal view of skull; Dogsthorpe, near Peterborough, UK; Lower Oxford Clay (Callovian); ×0·5.

Diagnosis. See Brown (1981*b*, p. 255).

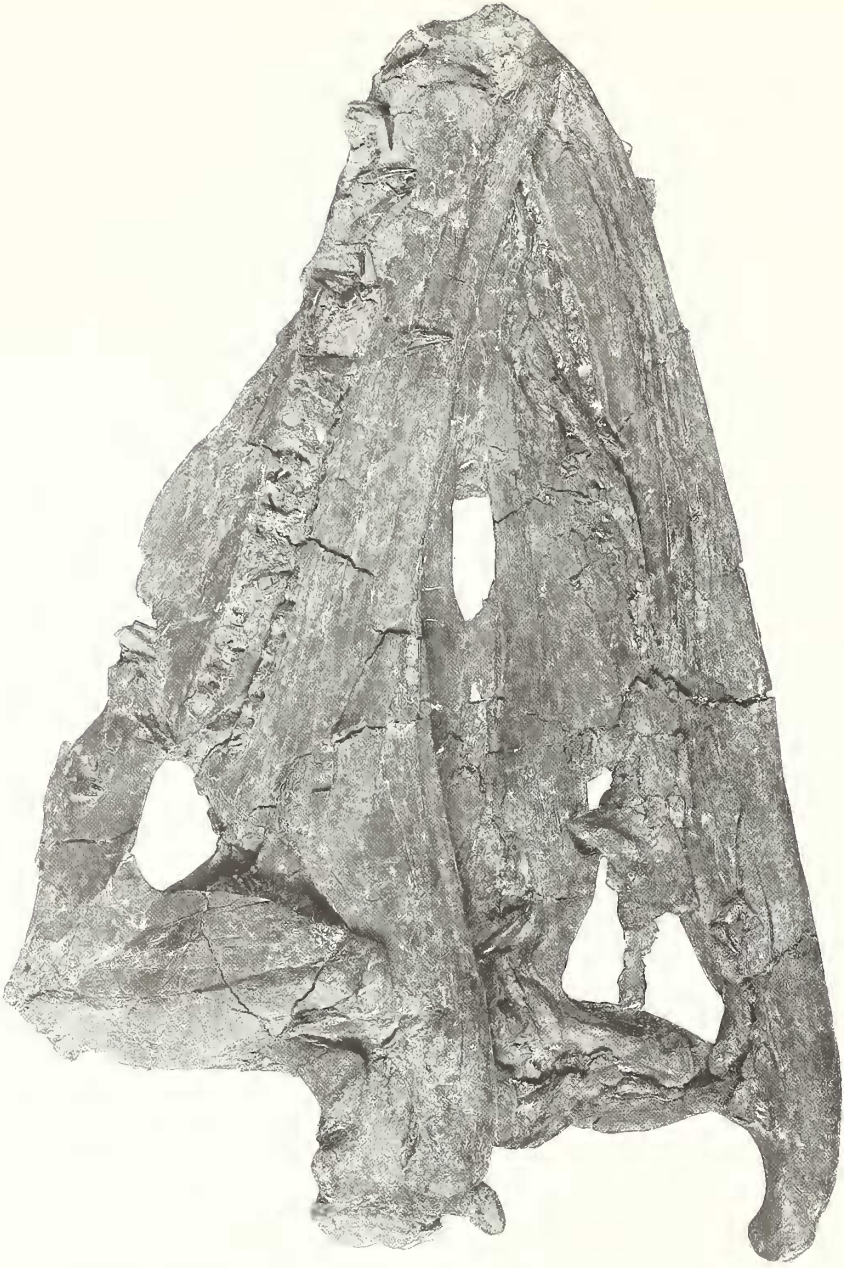<div align="center">

Cryptoclidus eurymerus (Phillips, 1871)

Text-figures 1–4

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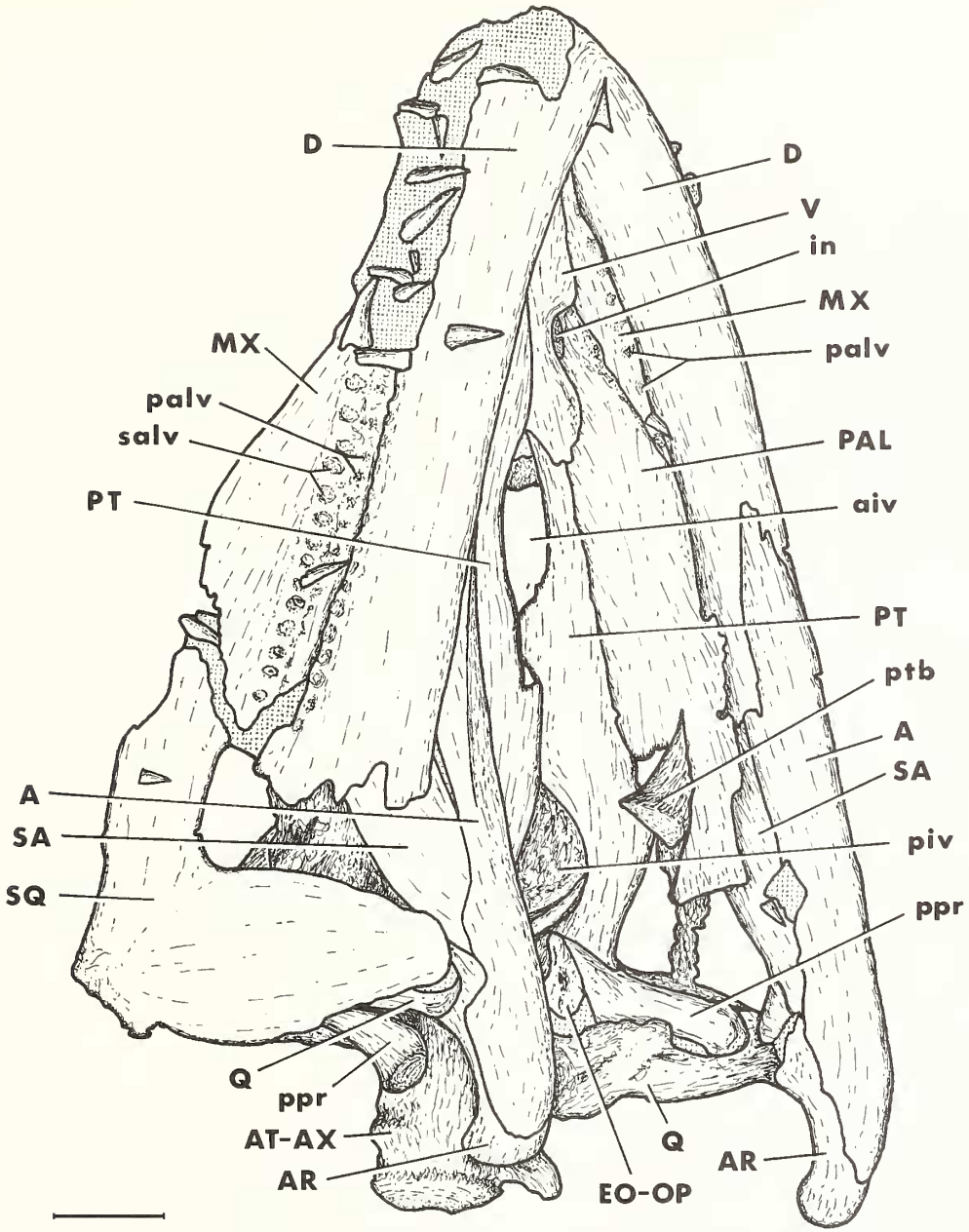*Synonymy.* See Brown (1981*b*, p. 256).

TEXT-FIG. 2. *Cryptoclidus eurymerus* (Phillips). Drawing of specimen in Text-figure 1, with residual matrix shown stippled. Abbreviations: A, angular; aiv, anterior interpterygoid vacuity; AR, articular; AT–AX, fused atlas–axis; BS, basisphenoid; D, dentary; en, external naris; EO–OP, fused exoccipital–opisthotic; EP, epipterygoid; F, frontal; fo, foramen; in, internal naris; J, jugal; L, lacrimal; l.PRO, left prootic; MX, maxilla; N, nasal; P, parietal; PAL, palatine; palv, primary alveoli; PF, postfrontal; pfo, pineal foramen; piv, posterior interpterygoid vacuity; PMX, premaxilla; PO, postorbital; ppr, paroccipital process of exoccipital–opisthotic; PRF, prefrontal; PT, pterygoid; ptb, pterygoid boss; Q, quadrate; QJ, quadratojugal; r.PRO, right prootic; SA, surangular; salv, secondary alveoli; SO, supraoccipital; SQ, squamosal; V, vomer. Scale bar represents 30 mm.

TEXT-FIG. 3. *Cryptoclidus eurymerus* (Phillips). PETMB R.283.412; palatal view of skull; Dogsthorpe, near Peterborough, UK; Lower Oxford Clay (Callovian); ×0·5.

Neotype. BMNH R2860, an almost complete adult skeleton from the Lower Oxford Clay of the Peterborough district (exact locality not known; see Andrews 1910, Brown 1981*b*). The fragmentary skull was hitherto the best specimen.

Diagnosis. See Brown 1981*b*, p. 255 (generic diagnosis: *Cryptoclidus*) and p. 257 (specific diagnosis).

TEXT-FIG. 4. *Cryptoclidus eurymerus* (Phillips). Drawing of specimen in Text-figure 3, with residual matrix shown stippled. Abbreviations as in Text-figure 2. Scale bar represents 30 mm.

Since the skull is known only for *C. eurymerus*, the cranial characters in both lists apply to the species.

Material. PETMG R.283.412 (accession number 307/1987), an almost complete skull and associated skeleton from Bed 10 of the Lower Oxford Clay, Dogsthorpe Brick Pit, near Peterborough (Grid Ref. TF 2130 0217).

Kosmoceras jason Zone (Calloman 1968; Martill 1985; Martill and Hudson 1991), Middle Jurassic, Callovian Stage.

<div align="center">DESCRIPTION</div>

General features

As preserved, the flattened specimen includes also the atlas-axis complex. The skull is approximately 335 mm long and 225 mm at its widest. The general appearance is shown in Text-figures 1 and 3, and analysed in Text-figures 2 and 4. The skull has suffered some post-mortem crushing and disruption of the elements. The left side of the skull table lies over the palate, with the posterior dorsal surface of the palate visible through the disrupted left orbit. On the right side the skull table is broken at the level of the jugal bar and folded under onto the ventral aspect, so that the right orbit cannot be traced. The mandibles and palate are almost complete. Most of the endochondral braincase elements can be identified but are largely obscured by overlying membrane bones. New information provided by this specimen permits the lateral skull reconstruction of *C. eurymerus* given by Brown (1981*b*, text-fig. 1) to be redrawn (Text-fig. 5).

Skull roof

The specimen shows the entire dorsal midline and left cheek region (Text-figs 1–2), and provides new information on the structure of the external naris, orbital margins and postorbital bar.

The suture of the left premaxilla with the maxilla runs to the anterior corner of the external naris, but behind this the specimen shows the naris bordered medially by the frontal and laterally by the maxilla. Posteriorly, the premaxillae have been displaced to the right by about 10 mm revealing the underlying anterior parts of the frontals, which show strong anteroposterior ridging on the area of the squamous overlap. When this post mortem displacement is reversed, the premaxilla covers the frontal; it may even have met the maxilla at the posterior corner of the naris, thereby excluding the frontal from narial contact when seen in dorsal view. In Text-figure 5, the frontal is depicted making a small contact with the naris and narrowly separating premaxilla and maxilla at this point. The external naris is slit-like and 25 mm long by 5 mm wide at the front. Crushing has obscured the internal detail.

The left premaxilla shows the six tooth sockets characteristic for *Cryptoclidus*. The number of maxillary alveoli is estimated to be about twenty; it is not possible to count them on either side, the left upper toothrow being obscured posteriorly by the overlying dentary whilst the right is obscured anteriorly.

The frontals are abraded on the orbital margins, and thus the orbital outline cannot be restored with confidence. In the midline, the frontals continue back to meet the parietals and largely enclose the pineal foramen, the parietals contributing only about one quarter of its margin. The pineal foramen is deeply recessed into an embayment formed by diverging anterior wings of the parietals.

The parietals form the usual high and narrow sagittal crest. The squamosals cover the highest point of this crest at the back, and meet in the midline. This region of the specimen was exposed before collection and is abraded.

The bones of the cheek region are relatively well preserved, especially on the left side; and the postorbital is seen for the first time in *Cryptoclidus*. It is a triangular element, extends far down into the temporal fossa, and forms a significant part of its border. On its posterior margin it is overlapped by the squamosal: halfway along this margin the union is interrupted by a small foramen. The anterior margin of the left bone appears complete, and has a marked, crenulated edge for most of its length, indicating that this is the suture line for the postfrontal. Therefore the postorbital lay mostly below and behind the postfrontal, and may have had only a small exposure to the orbital margin.

The element tentatively identified here as the left postfrontal is largely overlain by the postorbital and itself overlies the suture between frontal and parietal. The outline of the orbit is badly distorted, and the structure and relationships of the postfrontal are unclear.

The jugal is represented on the left by a fragment of bone, which unites with the squamosal and postorbital, and forms part of the margin of the infratemporal fossa. Growth lines on the surface of this fragment indicate that the jugal was vertically orientated, and was probably a small and weak strap-shaped bone extending squamously over part of the postorbital anterior to the preserved part. A broken section through the end of the anterior process of the right squamosal shows the very thin and laminate squamosal overlying an equally thin jugal with, underlying these two elements, the relatively massive postorbital forming the chief mechanical component of this region. On neither side is any part of the posterior margin of the orbit preserved; nor is there any evidence for the nature of the union of the jugal with the maxilla.

The large squamosal has the usual sauropterygian triradiate structure, and overlies the outer surface of the massive quadrate.

Palate

The palate is largely undisturbed with the left side fully visible, and is here seen in *Cryptoclidus* for the first time. The general arrangement of the palatal bones (vomers, large palatines and pterygoids) appears to be as normal for plesiosaurs; but ectopterygoids cannot be identified and may be missing from the specimen. The pterygoids are separated by large anterior and posterior interpterygoid vacuities; posteriorly their relationship to the basis cranii and to the quadrates, both variable plesiosaurian characters, cannot be seen. There is no evidence for the existence of suborbital fenestrae; the lateral margins of the palatines are very thin and abraded but nevertheless intact, and the extent and continuity of abraded bone indicates strongly that they were absent.

The juxtaposition of the left internal and external nares can be observed on the specimen. The internal nares lie a few millimetres in advance of the external nares, the separation being greater on their posterior margins. Fine osteological details are not preserved.

Braincase

The disarticulated endochondral elements of the braincase are partly hidden dorsally by the bones of the skull roof and cheek, and in ventral view by the posterior part of the right mandibular ramus and the quadrate and squamosal. Both quadrates, fused exoccipital–opisthotic elements and the prootics together with the supraoccipital and the left epipterygoid may be identified (see Text-figs 2 and 4); but full description would be possible only by removing the overlying membrane bones and undertaking further preparation. The atlas and axis are preserved in articulation with the occiput.

Mandibles

The right outer surface and left inner surface of the mandible are well displayed (Text-figs 3–4). The ventral edge of the left ramus is undisturbed and shows a straighter profile than previously reconstructed. Some post-mortem displacement has occurred between elements of the right ramus. There is no evidence for coronoid or prearticular elements, which seem to be absent in the species; neither is there any splenial, which to date has been identified only tentatively from fragments in a single skull (R8621; Brown 1981*b*, p. 264).

There are certainly twenty-six and possibly twenty-seven tooth positions. The dentition is represented by numerous teeth or tooth fragments both *in situ* and detached. The teeth show the characteristic reduced ornamental pattern diagnostic of *Cryptoclidus* (see Brown 1981*b*, fig. 5).

RECONSTRUCTION

The lateral skull restoration given by Brown (1981*b*, fig. 1) was based upon the fragmentary neotype skull (BMNH R2860) with the addition of tooth-row details from other specimens. Outlines of much of the snout including the external nares and the postorbital and jugal bars were conjectural. Specimen PETMG R.283.412 permits an objective restoration of the snout and external naris, adds details of the postorbital and jugal, and shows an undistorted mandibular profile. However, overall skull shape reconstruction cannot be improved. Text-figure 5 has been produced by modifying the 1981 restoration with respect to the above features of the new specimen. The orbital outline and the anterior extent of the postfrontal and jugal remain conjectural.
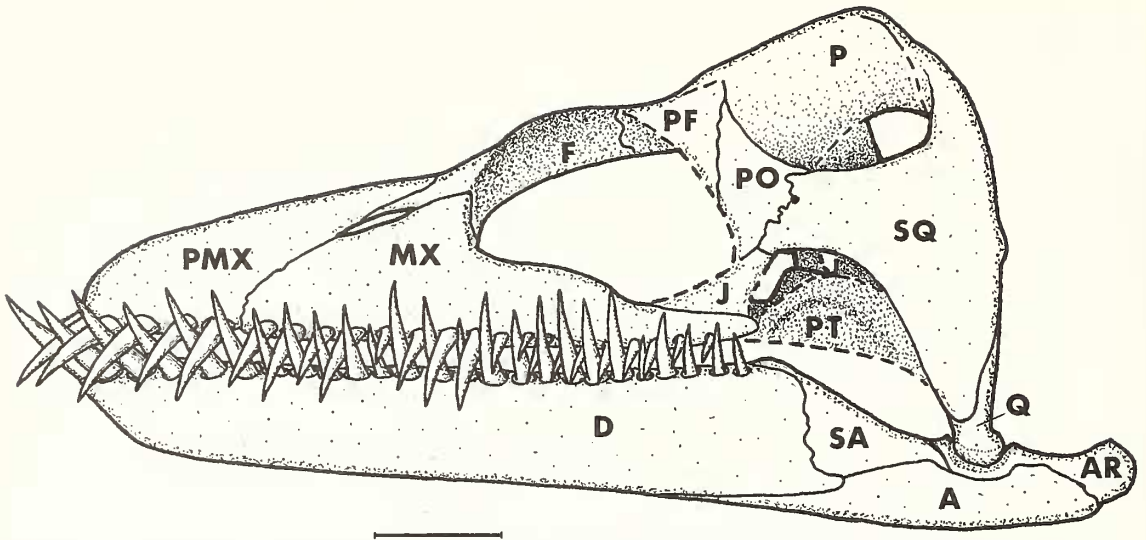
TEXT-FIG. 5. *Cryptoclidus eurymerus* (Phillips). Lateral restoration of skull after Brown (1981*a*, fig. 1), modified to show new osteological details from PETMG R.283.412. Scale bar represents 30 mm.

DISCUSSION

The cryptoclidid cheek

Brown (1981*b*, figs 1, 22, 29) reconstructed lateral views of the skulls of *Cryptoclidus*, *Tricleidus* and *Kimmerosaurus*, with the jugal shown as a narrow vertically orientated bar separating a large orbit from the infratemporal fossa. This pattern is at variance with reconstructions of Cretaceous elasmosaurid genera given by Welles (1949, 1952, 1962; see for example Text-fig. 6E), the restoration of the Upper Liassic species *Plesiosaurus guilelmiimperatoris* drawn by Fraas (1910, fig. 1), and the reconstruction of *Muraenosaurus* given by Andrews (1910, fig. 46b). In all of these the jugal is a large quadrilateral element, with a horizontal long axis, small borders on orbit and/or infratemporal fossa and a long suture dorsally with the postorbital. Brown's evidence for this configuration was inferred by the necessity to restore the anterior end of the squamosal in the best of the skulls which he reviewed (that of *Tricleidus*) in a position spatially well above the posterior end of the maxillary tooth row, and by the close resemblance of the form of the squamosal in *Cryptoclidus* and *Kimmerosaurus* to that of *Tricleidus*.

The first objective evidence supporting this cheek configuration in any plesiosaur was provided by Brown *et al.* (1986) for *Kimmerosaurus*. Chatterjee and Small (1989) described the new cryptoclidid genus *Turneria*, and in a tentative restoration (Chatterjee and Small 1989, fig. 2) showed a similar configuration. The new *Cryptoclidus* skull described above now provides objective evidence for the same cheek pattern in this genus also. Brown (1994) revised his classification of plesiosauroid families and genera; the 'vertically-orientated jugal bar separating orbital and infratemporal fossa margins' is made a diagnostic character of the family Cryptoclididae, and he includes *Tricleidus* (listed as an elasmosaurid in Brown 1981*b*) as a cryptoclidid genus.

Sauropterygian cheek and orbit evolution

Text-figure 6A shows the primitive diapsid cheek and orbital structure from which the various sauropterygian patterns (Text-fig. 6B–F) must be derived. The jugal is a large element of the circumorbital series linking the lacrimal to the postorbital, and thereby excluding the maxilla from the orbital margin. It meets the quadratojugal posteriorly and with it forms the lower temporal arch.
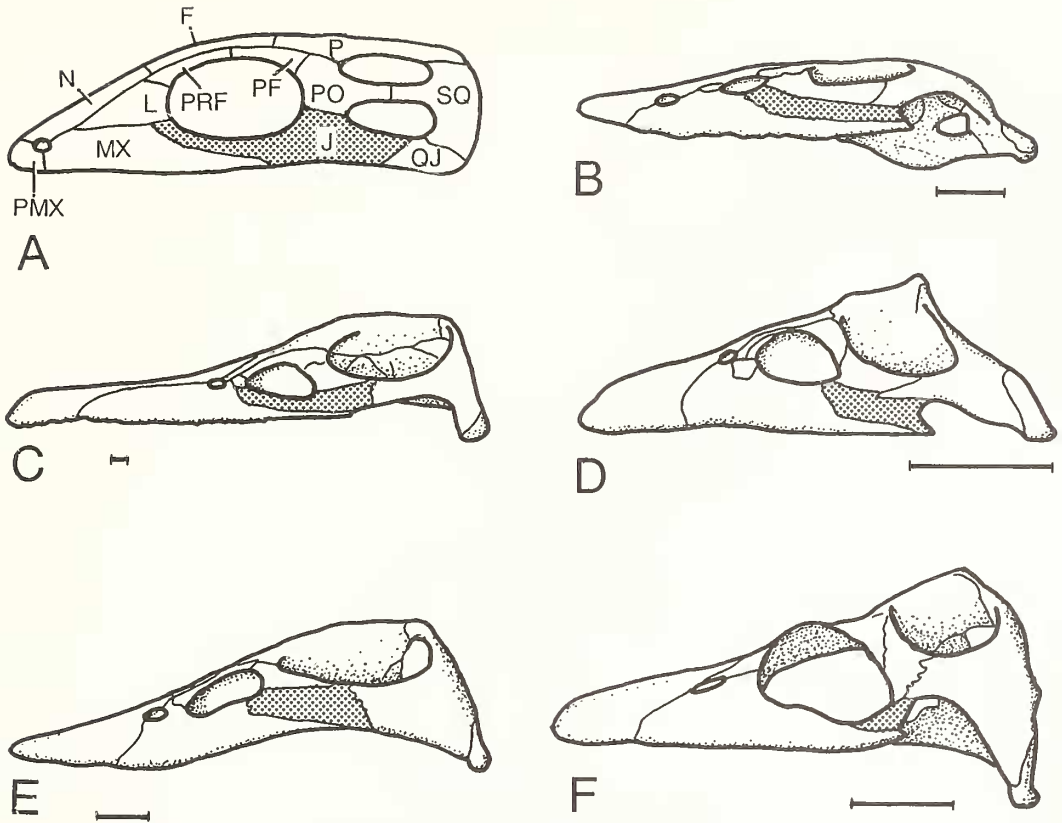
TEXT-FIG. 6. Representative sauropterygian skulls. Jugal shown stippled. Scale bar represents 50 mm. A, generalized primitive diapsid, redrawn from Romer (1966, fig. 155d). B, a nothosaurid (*Siuosaurus*), redrawn from Storrs (1991, fig. 33c), after Huene (1921). C, a pliosaurid (*Pliosaurus brachyspondylus*), after Taylor and Cruickshank (1993, fig. 5). D, a plesiosaurid (*Plesiosaurus brachypterygius*), after Huene (1923, pl. 2, fig. 1). E, an elasmosaurid (*Styxosaurus snowii*), after Welles (1952, fig. 5). F, a cryptoclidid (*Cryptoclidus euryuerus*), reduction of Text-figure 3.

In the upper temporal arch the postorbital intervenes between the jugal and the anterior process of the squamosal.

In the Sauropterygia, the quadratojugal has been lost and the posterior part of the jugal remodelled. This results in absence of the lower temporal arch; but a deep ventral excavation of the lower cheek margin in nothosaurids, plesiosaurids and cryptoclidids (Text-fig. 6B, D, F) bears witness to the former presence of a lower temporal opening. Additionally, the anterior process of the squamosal has made contact with the jugal, excluding the postorbital from the new ventral cheek margin.

In the pliosaurid *Pliosaurus brachyspondylus* (Text-fig. 6C), the elongate jugal retains contact with the lacrimal anteriorly as in the diapsid ancestor (Taylor and Cruickshank 1993); and a similar contact of jugal and lacrimal, hidden from lateral view within the orbit, was described in the nothosaurid *Paranothosaurus* by Kuhn-Schnyder (1964) (see Storrs 1991, p. 144). In other nothosaurid and pliosaurid genera the jugal and lacrimal separate, and the lacrimal may be lost or more probably may be fused to the maxilla (as in *Rhomaleosaurus megacephalus*; Cruickshank 1994) resulting in a contact of the maxilla with the orbit.

In plesiosauroid genera the snout is shorter, the orbit is proportionally enlarged, the maxilla forms the major part of the lower orbital margin, and the jugal is shortened. In plesiosaurids and

elasmosaurids (Text-fig. 6D, F), in which orbital enlargement is moderate, the jugal is quadrilateral with a horizontal axis. In cryptoclidids (Text-fig. 6E) there is a substantial increase in the relative size of the orbit, involving also a lateral rotation of the maxillary flange carrying the orbital margin outward (not clearly depicted in lateral restorations); and in addition the ventral cheek excavation is not only retained but possibly enlarged. The cryptoclidid jugal becomes elongated along its vertical axis so as to form a narrow bar separating the enlarged orbit from the margin of the infratemporal fossa.

The characters of the sauropterygian cheek and orbit are analysed phylogenetically in Text-figure 7. The inclusion of further character analysis is beyond the scope of the present work, and is largely
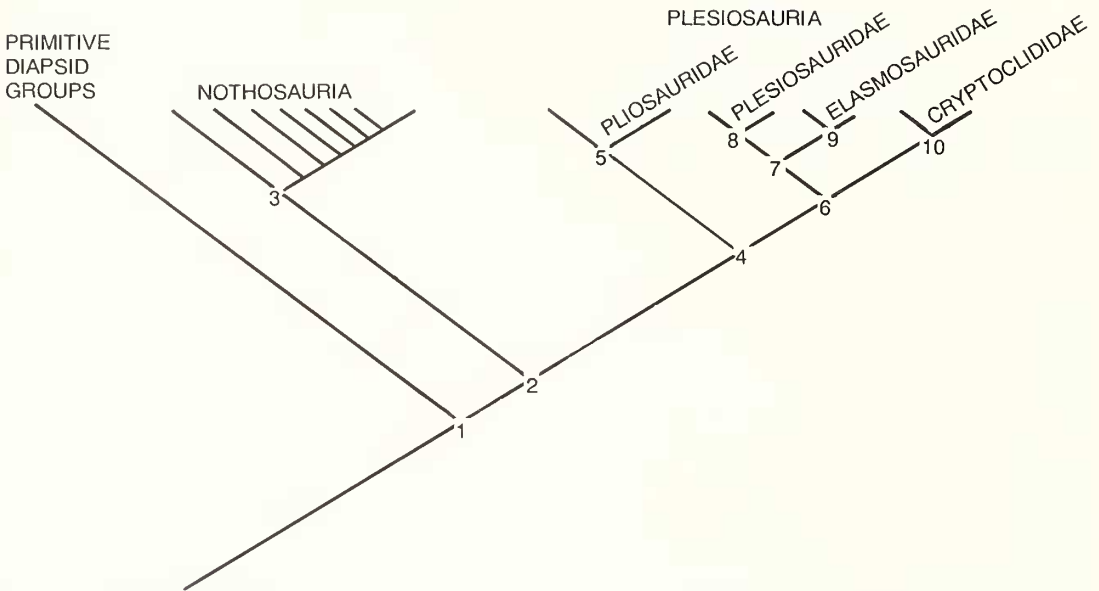
TEXT-FIG. 7. Phylogenetic analysis showing interrelationships of major sauropterygian groups, based on characters of the cheek and orbit. Numbered nodes 1 to 10 are characterized in the text.

dependent upon the results of an ongoing review of Lower Jurassic genera involving several workers. That review is almost certain to overthrow the present superfamily and family divisions of the Plesiosauria. Shared derived characters of cheek and orbit uniting the groups of the current classification are as follows.

Node 1 (*outgroup: primitive diapsid*). Lower temporal bar present. Jugal contacts lacrimal anteriorly and is separated from squamosal by postorbital.

Node 2 (*Sauropterygia*). Loss of quadratojugal breaks lower temporal arch; a deep ventral excavation of the lower cheek margin results, and quadrate becomes visible laterally. Jugal contacts squamosal.

Node 3 (*Nothosauria*). Contact between jugal and lacrimal retained within orbit in some; contact lost in others, with maxilla intervening.

Node 4 (*Plesiosauria*). Cheek/orbit characters as in Node 2.

Node 5 (*Pliosauroidea, Pliosauridae*). Progressive reduction in ventral cheek excavation. Contact between jugal and lacrimal retained and visible laterally in some; contact lost in others, with maxilla intervening.

Node 6 (*Plesiosauroidea*). Snout shorter than at Node 2, with proportionally larger orbit. Contact of jugal and lacrimal lost, maxilla intervenes and forms the major part of the lower orbital margin.

Jugal quadrilateral with horizontal long axis and short contacts on orbital and ventral cheek margins.

Nodes 7 and 8 (*Plesiosauridae*). Cheek/orbit characters as in Node 6.

Node 9 (*Elasmosauridae*). Reduction of ventral cheek excavation.

Node 10 (*Cryptoclididae*). Orbit proportionally larger than in Node 6. Deep ventral excavation of cheek margin retained and perhaps increased. Jugal reduced to a narrow vertically-orientated bar separating orbit from ventral cheek margin.

Using characters only of the cheek and orbit, it would be equally parsimonious to link Nothosauria and Pliosauridae as a sister group of the Plesiosauroidea. In preparing Text-figure 7 we have borne in mind many other characters, such as those associated with marine adaptation of the postcranial skeleton, which firmly unite the Pliosauridae with the Plesiosauroidea.

Olfactory system

Cruickshank *et al.* (1991) and Cruickshank (1994) described the structure of the internal and external nares in *Rhomaleosaurus megacephalus* (Stutchbury), and concluded that this pliosaurid possessed a unique system of underwater olfaction. Water entered the mouth at or near the premaxilla–maxilla suture, and then passed to the anteriorly-placed internal nares. It was then sucked over the olfactory epithelium and out of the more posteriorly-placed external nares by hydrodynamic forces generated by the forward movement of the animal. The internal nares in *Cryptoclidus* are anteriorly placed with respect to the external nares as in *Rhomaleosaurus*, and on that basis a similar mechanism may be invoked for *Cryptoclidus*. Use of this mechanism seems to be a constant feature of the Plesiosauria (Taylor and Cruickshank 1993; Cruickshank 1994).

Jaws and feeding habit

By comparison with pliosauroid skulls, such as that of *Rhomaleosaurus zetlandicus* (Phillips) (see Taylor 1992), the skull of *Cryptoclidus eurymerus* is more lightly built. It lacks structures such as the large pterygoid flange; the suborbital fenestra (site of insertion of an enlarged anterior pterygoideus muscle); thick very strong teeth, and construction of the lower jaw as a stout beam resistant to substantial torsional loads; all of which Taylor (1992) explained in terms of a twist-feeding predatory habit in *Rhomaleosaurus*. Clearly *Cryptoclidus* did not feed in this way. The increased number and decreased size of the teeth by comparison with plesiosaurids and elasmosaurids is not as marked in this genus as in more advanced cryptoclidid genera such as *Kimmerosaurus* Brown; but it seems likely that the prey was nevertheless small and relatively soft, perhaps including soft-bodied cephalopods and small fishes. The general structure is compatible with a filter-feeding habit suggested for cryptoclidids by Brown (1981*a*), and resembles that of modern 'krill' feeders described by Massare (1987). The mandible in *Cryptoclidus eurymerus* lacks the prearticular and the coronoid. Both these elements are present in primitive pliosauroids (Taylor 1992; Cruickshank 1994), and *Tricleidus* Andrews (now included in the Cryptoclididae as a primitive genus: Brown 1994) retains a much-reduced coronoid (Andrews 1910) but has lost the prearticular. It would appear that the prearticular and coronoid help to brace the dentary to the postdentary bones, since in pliosaurs (and also in the one skull of *Tricleidus*) the mandible is invariably preserved as a single structure; whereas in *Cryptoclidus* (present paper; Brown 1981*b*) and *Kimmerosaurus* (Brown 1981*b*; Brown *et al.* 1986) it is usual to find the dentary displaced with respect to the postdentary elements. This feature of preservation further demonstrates the difference in torsional strength related to differing feeding habits between pliosauroids and cryptoclidids.

Thursfield took the photographs reproduced in the text-figures. Gordon Chancellor of Peterborough City Museum and Art Gallery suggested that the work of preparation of the skull be undertaken in Leicester, and obtained the Geologists' Association grant which covered that expense. Mike Taylor and Dave Martill provided valuable discussion on aspects of plesiosaurian palaeontology and taphonomy.

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